

# The Positive Interactions in Agroecosystems

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It has been 30 years since Eugene Odum rescued the term *ecosystem* from relative obscurity and set in motion the modern study of ecological systems. In his book *Fundamentals of Ecology* (1953) Odum used the ecosystem concept as an organizing principle, in contrast to the autecological-ecophysiological approaches prevalent at the time. The ecosystem approach gave scientists guiding principles through which environmental problems could

be effectively addressed. Autecology does not provide the tools needed to deal with large-scale environmental issues, be they radioactive fallout or abuse of agricultural chemicals. As Odum emphasized, an ecosystem is a functional entity that is more than the sum of its parts. Knowing the properties of the parts does not adequately predict the behavior of the whole.

Odum's holistic approach was timely; since the late 1950s, awareness of rapidly deteriorating environmental quality had been increasing; urgently needed decisions affecting whole systems had to be made. With the coming of age of ecosystem ecology in the 1960s, regulations governing chemical releases and usages could be developed. Their impact was especially pronounced in agriculture. Today, the importance and usefulness of the holistic approach and the urgency of preventing further environmental deterioration are still pertinent for modern agriculture.

The term *ecosystem* has been used in a variety of ways; the term *agroecosystem*, a result of applying ecosystem concepts to agriculture, has been particularly variable. Like other authors, we feel obliged to discuss it and to define how we use it here. All ecosystems on our planet are more or less open, exchanging abiotic and biotic elements with other ecosystems. Agroecosystems are designed to be extremely open, with major exports of primary or secondary production. Modern agroecosystems are entirely dependent on human intervention; without management agroecosystems as such will not persist. For this reason they are often designated as artificial ecosystems as opposed to natural systems, which do not require man's management. In fact, the great majority of our so-called natural systems—forests, rivers, lakes—are managed so that the distinction between natural and artificial is no longer clear. Definitions of agroecosystems often include an entire support base of energy and material subsidies, seeds and chemicals, and even a sociopolitical-economic matrix in which management decisions are rooted. That is no doubt logical, but we prefer to designate the individual field as the agroecosystem because this is consistent with designating and studying an individual forest catchment or a lake as an ecosystem. We envision the *farm system* as consisting of a set of agroecosystems—fields with similar or different crops—together with the support mechanisms and socioeconomic factors contributing to their management. Use of individual field units as agroecosystems is the approach we have taken in studies at the University of Georgia. There we are applying methods of ecosystem sampling and analysis in order to answer an initial, essential question: Are agroecosystems mere collections of components managed by man, or do they retain the functional properties of natural ecosystems—nutrient conservation mechanisms, energy storage and utilization patterns, and regulation of biotic diversity? The answer seems to be in the affirmative, at least for the systems in Georgia (Stinner et al., in press).

Analysis of ecosystems has centered on measurements of three general types of phenomena: species richness in various components; functional properties such as energy flow and nutrient cycling; and more recently, ecosystem response to perturbation (Botkin, 1980). A fourth phenomenon, likely to be important, is allelochemical regulation (Rice and Pancholy, 1973). In this analysis we will focus on the positive interactions among components of ecosystems. By positive interactions we mean those that generally lead to the maintenance of functional integrity, biotic persistence, and self-regulation. In contrast, negative interactions would be those that lead to deterioration of biotic persistence and loss of functional integrity. In order to promote efficient resource use coupled with persistence of the systems through time, agroecosystem management of the future will attempt to benefit from such positive interactions. We equate positive interactions with cooperative relationships among organisms, where interaction is mutually beneficial. Some modern agronomists perceive noncrop organisms as exclusively antagonistic. We suggest that the designations between antagonistic and cooperative interactions exist in a continuum, and that management practices may determine the prevalence of one or the other.

Figure 1 contrasts the relationships between components for natural and agricultural ecosystems. Figure 1A illustrates nutrient flow between major components of a natural ecosystem. Figure 1B shows how nutrient flows are changed by management activities. Transfer from primary producers to consumers is reduced by applications of insecticides (shown as a control element in Fig. 1B). Transfer from primary producers to the decomposition subsystem is regulated by herbicides and cultivation during the growing season, changing the timing of inputs to the decomposers. At season's end the primary producers may be mowed down, providing massive pulse to the decomposers. The decomposition subsystem itself is inadvertently regulated both by application of pesticides and by cultivation. Plowing incorporates crop residues into the mineral soil, speeding their decomposition rates.

The overall impact of these regulatory measures is to upset the normally conservative nutrient cycles by increasing rates of nutrient release to the abiotic phase. In Figure 1B we show a relatively large nutrient influx (fertilizer) and export of primary production. As a consequence of high influx and disturbance of ecosystem function, a relatively large nutrient loss (runoff or "nonpoint pollution") is suggested.

The four-compartment model of Figure 1 is an oversimplified abstraction of ecosystem nutrient cycling, but it does serve to illustrate the negative impact of some management technologies. Self-regulatory properties, prominent in natural systems, are altered or suppressed in agricultural systems. Within-system interactions may not differ in kind, but certainly differ in degree. In the following we will briefly consider some of the positive interac-

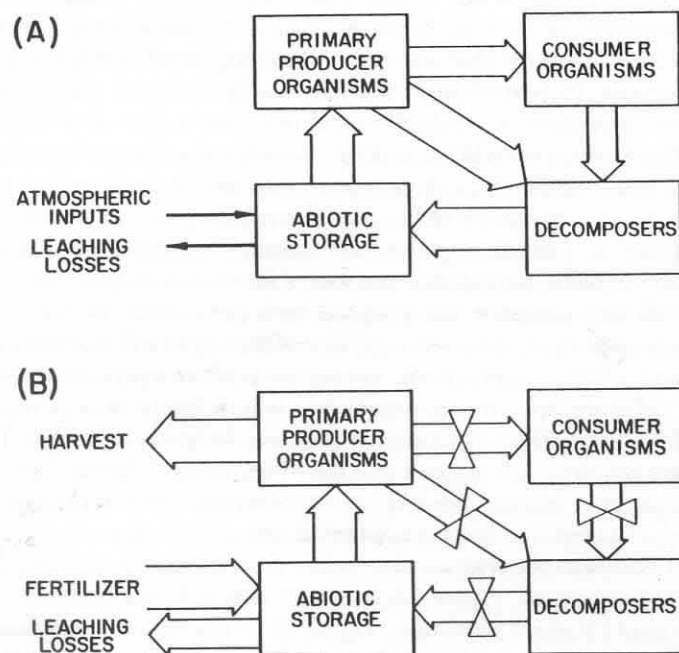


**Figure 1.** Nutrient circulation through major components of (A) natural ecosystems and (B) agroecosystems. In natural systems internal cycling of nutrients greatly exceeds flowthrough expressed as atmospheric inputs and leaching losses (top). In agroecosystems management techniques include control of consumer organisms with insecticides, control of primary producers with herbicides as well as cultivation and harvest, and control of decomposition through cultivation and plowing. Fertilizer becomes the major nutrient input to the agroecosystem, and harvest constitutes a major output, but leaching losses become larger also.

tions characteristic of agroecosystems, that is, those which tend to increase self-regulation of processes. We suggest that agroecosystem management of the future will attempt to incorporate such positive interactions into modified management practices.

### PRIMARY PRODUCERS

In field crop agroecosystems, crop monoculture is a goal seldom achieved. Weeds are generally viewed as competitors for water, nutrients, or sunlight, or at least viewed as nuisances. Ecologists have observed that weed species often have some predictable biological characteristics such as resistance to climatic extremes, high reproductive and dispersal capacities, and allelo-

pathic chemicals. The autecology of weed species is a rapidly developing research area (Harper, 1960). Since weed-free fields are unusual, it follows that most crop plants can tolerate weeds at low densities without dramatic yield reductions. Are there, in fact, positive interactions—mutualistic associations—between weeds and crop plants? A few tentative suggestions have been made (Sagar, 1968; Tripathi, 1977). Elimination of present-day weeds might open a niche available to even better competitors. Present-day weeds and crop plants may have evolved a mutual tolerance, if not a true mutualism (Maun, 1974). Elimination of weeds might increase certain pest problems (see below) and can contribute significantly to erosion problems, especially in the early growth and post-harvest period. These suggestions are largely speculative. It does appear that weeds constitute a significant nutrient reservoir in agroecosystems. Where competition for nutrients is not limiting, weedy growth can retain nutrients that might otherwise be lost from the agroecosystem (Stinner et al., in press). In some cases weed species may promote nitrogen fixation. The value of weeds for manipulation of beneficial insect populations (Altieri and Whitcomb, 1979) is increasingly suggested.

A philosophy of beneficial weed control could evolve in a manner similar to that of insect control. That is, the treatment of insect problems evolved from a strategy of complete insect control to a perspective of tolerance of some pests in low numbers. Economic and environmental considerations may modify the popular attitude that total weed control through chemical application is essential. Concurrently, management practices could progress toward techniques that encourage certain weed species, once beneficial interactions between crops and weeds become understood (Altieri and Whitcomb, 1979). Interplanting practices furnish an example of what may be regarded as progress in this direction; once considered too troublesome to use in large monocultures, the practice is currently gaining in popularity (Trenbath, 1981).

## CONSUMERS

Because of their potential economic importance, insect herbivores in crop systems, and their responses to management practices, have been ecologically well defined. Except for pollinators, insect herbivores as a group are generally viewed as undesirable; the insect-free field, however, has been virtually impossible to obtain. Below, we outline interactions within the consumer community itself; specific insect-plant interactions will be considered in a subsequent section. Competition between herbivore insect species is often considered a major factor for shaping the structure of their

community, but the magnitude of its effects has been overemphasized. Even in agricultural fields, primary consumption is seldom so high as to suggest food as a limiting resource. On a global scale, for instance, crop losses to insects before harvest have been estimated at 14% (Perkins, 1982).

Chemical control measures aimed at one or a few consumer species are not the sole determinants of species composition of the community. Barrett (1968) found that diversity was increased by a single insecticide application. Even after repeated attempts at chemical control, faunal diversity in crop fields may be high. Yet the significance of this diversity is largely unknown. For example, do these diverse arthropod communities include the potential for maintaining pest insect species below economic thresholds? It is probable that insect populations in a given agroecosystem are more strongly influenced by characteristics of surrounding ecosystems than by field-specific factors. Stinner et al. (1982) point out how vagile many pest species are and stress the importance of the matrix of crop fields and regional agricultural practices as determinants of community species composition. Such extrinsic factors may favor diversity not only of the consumers but may also play a role in maintaining predator-prey complexes. Integrated pest management (IPM) takes advantage of these to hold primary consumption to acceptable levels. While IPM uses a combination of means, TPM, or total pest management (Perkins, 1982), embodies the notion of complete eradication of pest species. As Perkins (1982) points out, both approaches seized upon ecological principles and the term *integrated* to characterize their efforts.

## PRODUCER-CONSUMER INTERACTIONS

Insect-plant coevolution is a major unifying theme in insect ecology today. Often, it is viewed as a set of antagonistic exchanges in chemical warfare. Evidence for mutualism between plants and insects—positive interactions—is becoming more convincing (Owen, 1980; Owen and Wiegert, 1976; Petelle, 1982; Thompson, 1982). In agricultural systems the term *beneficials* is used to denote predators and parasites that may reduce pest insect populations. Altieri and Whitcomb (1979) have presented the argument that weeds are important in the biology of many of the beneficial insects. They suggest field management techniques to take advantage of this relationship and maximize numbers of beneficial insects. Aside from pollination, there have been few demonstrations of the value of herbivory to crop plants. However, Hilbert et al. (1981), McNaughton (1979), Dyer (1975), and others have argued that a low level of grazing may increase net primary production—that there is an optimal level of grazing in ecosystems. Evidence cited includes increased photosynthetic rates following grazing, reallocation of photosyn-

thate, increased tillering or other elaboration, better light penetration, and a variety of indirect mechanisms.

Usually, any consumption of crop plants is considered to be antagonistic, even at relatively low levels. However, some consumption may be beneficial to crops. Compensatory growth following herbivory is well documented (Hills and Peters, 1971; Barner and Fletcher, 1974; Crossett et al., 1975). In field crop systems the exact nature and extent of plant-insect mutualism remains to be explored.

## DECOMPOSITION AND SOIL

Soil—its structure, nutrients, and organic matter—is the major determinant of primary production in many regions. Yet, the ecology of the soil—the belowground ecosystem—is still relatively unknown.

From the viewpoint of nutrient dynamics in agroecosystems, soil is the major nutrient storage reservoir. As in other ecosystems, the complex interactions between roots, microbes, and animals contain both positive and negative elements (Curl, 1982), with the soil fauna acting as regulators rather than active decomposers. The burgeoning literature on mycorrhizal fungi indicates that plant-fungus mutualisms may be of considerable importance for agricultural crops. Dissemination of mycorrhizal spores by arthropods points to the importance of both mutualistic associations and indirect regulation. There is some evidence that soil arthropods may play a significant role in dispersing mycorrhizal propagules (Rabatin and Rhodes, 1982).

In agroecosystems chemical and mechanical disturbances influence both biotic and abiotic components of the decomposition subsystem, and their effects are superimposed on normal faunal and floral phenological cycles. The impact of various tillage practices on soil biota are not always clear-cut, however (Loring et al., 1981; Moore et al., in press). Research in no-tillage systems may hold the greatest promise for identifying positive interactions within the soil. In general, no-tillage provides a more favorable environment for soil-litter biota: crop residues are left on the soil surface, reducing moisture loss and providing relatively continuous substrate for decomposers; organic matter input is more gradual, as is nutrient release; faunal interactions are probably more pronounced and more significant in regulating decomposition rates under no-tillage conditions. Root growth, in turn, can be enhanced by increased invertebrate animal activity (Edwards and Lofty, 1977).

Weeds and weed residues, suppressed by conventional tillage practices, act as temporary nutrient reservoirs in no-tillage systems. Residue management research should uncover interactions between crops and weeds that

are beneficial to crop-nutrient dynamics, but many of the intermediate coupling processes remain to be quantified.

This brief characterization of the positive interactions in agroecosystems suggests that mutualistic relationships are extensive, even in field crop agroecosystems. We predict that the identification of positive interactions in agroecosystems will continue to grow. These mutualistic interactions are characteristic of ecosystems with self-regulating capacities. They indicate that the term ecosystem is quite appropriate for field crop systems and that agroecosystems differ in degree, but not in kind, from other ecosystems.

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